

Multi-stemming and mechanics of trees and shrubs growing along avalanche paths

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Abstract

We measured dynamic modulus of elasticity (E_d) and bending strength (σ) for several tree species growing in or around an avalanche path in the French Alps. Species were single- or multi-stemmed, the latter being more abundant at the centre or edges of the path. *Alnus viridis*, generally found at the centre of avalanche paths, had the lowest E_d and σ , and was strongly multi-stemmed, thus allowing this species to bend during an avalanche or to resprout if damaged. In several species where stem bases were procumbent after snow damage, E_d increased with height up the stem, conferring a mechanical advantage on these young stems which need to grow quickly upwards and dominate the canopy. E_d did not change along stems in *Corylus avellana*, a multi-stemmed shrub with stems often leaning on each other, thus providing mutual support, as also found in semi self-supporting plants.

Introduction

Whereas competition between species has traditionally been considered the driving process for selection and diversity, it is now postulated that in a world experiencing climate change and frequent human impacts in ecosystems, disturbance may become the driving process. Disturbance of a habitat may be abiotic (flooding, storms, fire) or biotic (grazing, insect outbreak). Plant resistance and resilience to disturbance can be reflected in a certain number of traits, including responses to nutrient and water availability, temperature and light. In the case of mechanical, abiotic disturbance often occurring on mountain slopes e.g. storms, landslides and avalanches, plant mechanical properties may determine whether or not a species will be adapted to the disturbance, depending on its frequency and intensity [1].

Avalanche paths provide specific habitats for a number of species, and are now recognised as rich in plant diversity [2]. If avalanches are to be avoided e.g. in populated areas, barriers are usually placed in the departure zones. However, the use of protection forests to stabilize the snow mantle at departure zones is now being explored in detail [3], although once an avalanche is underway, the energy needed to fracture and transport a dense forest of spruce trees is very small compared with the kinetic energy of a large avalanche [4]. The ability of a given species to fix the snow mantle is thus of interest, but opinions are conflicting as to which species confer the best protection against snow movement. Single-stemmed conifers which are >2.0x taller than the depth of the snow are considered as best at stabilizing the snow mantle [3]. With regard to multi-stemmed species which do not reach this target height, it has been conjectured that they offer either no protection or even exacerbate avalanches as the snow held on branches can be released suddenly if the stems straighten up quickly, although under what conditions this may occur is not specified [5]. Avalanches in turn can cause uprooting and overturning of trees. Therefore, for a tree species to grow in an avalanche path, a certain number of strategies would increase its survival and persistence.

To resist mechanical failure due to an avalanche, stems should be small and flexible enough to bend under the weight of snow. Large stems typically break [6]. Even if stem breakage does occur, the

ability to resprout from the stem or stem base would improve survival of an individual, especially if the plant was well-anchored. The resprouting ability of a species depends on the type and time of disturbance throughout the year, as well as tree size [7,8].

We measured dynamic modulus of elasticity (E_d) and bending strength (σ) for several tree species (Table 1) growing in or around an avalanche path in the French Alps. Each species possesses a different ability to resprout, therefore influencing growth form of the individuals from which the samples were taken. *A. viridis* is typically found at the centre of the path, *F. sylvatica* and *C. avellana* at the periphery of the path and *A. incana* and *B. pendula* at a distance from the path or downslope of the path. An inventory of stem form for all species present was made in several transects along the avalanche path and the consequences of multi-stemming on mechanical properties discussed.

Material and methods

Tree species, number, vertical height, diameter at 1.3m (DBH) and the number of stems present per individual (Table 1) were determined in six 100m x 4 m transects, traversing an avalanche path (Combe Gilbert) at Allemont, Isère, French Alps. When more than one stem was present per individual, the mean DBH was calculated for the stems with a maximum of five stems measured. The avalanche path was approximately 600 m long and 21 avalanches have occurred over the last 45 years (<http://www.avalanches.fr/>). A major mudslide occurred in 1952, and natural regeneration has since occurred in a cone shape (Fig. 1). In March and April 2009, dormant stems were cut from individuals at the centre or the edges of the avalanche path at four different altitudes. These samples were immediately transported to the laboratory for mechanical analysis, kept moist at a temperature of 4°C and tested within 4 weeks.

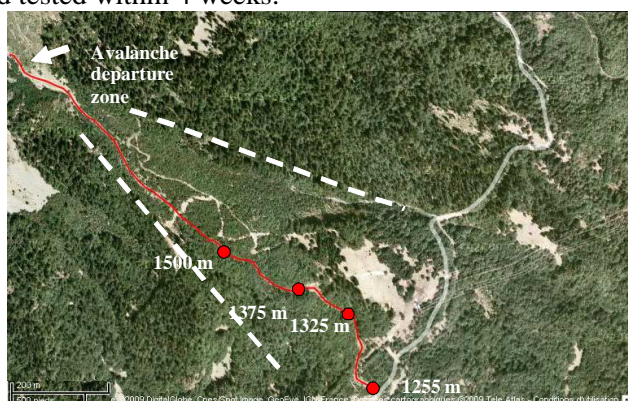


Fig. 1 Wood samples were taken at four altitudes along an avalanche path (solid line) at Allemont, Isère, French Alps. The path lies in an area where a rock- and mudslide occurred in 1952. Natural regeneration has since taken place, consisting mainly of broadleaf species (within the cone-shaped area bordered by dashed lines). Image courtesy of GoogleEarth.

Bending strength (σ) for stem segments for five species (Table 1) was determined using standard 4-point bending tests (European norm NF EN 408).

Dynamic modulus of elasticity (E_d) was measured in samples taken from *C. avellana*, *A. viridis*, *F. sylvatica* and *B. pendula*. Stems from individuals were cut into sections and the distance between the mid-point of the section and the tree base measured. Only samples from the main stem were measured, not side branches. We used the acoustic method, WISIS [9] to measure E_d . The WISIS system was designed by CIRAD as a nondestructive device to evaluate the mechanical state of in-service solid wood members in structure (<http://www.xylo-metry.org/en/wisis.html>). WISIS measures, among other parameters, E_d using a time of flight technique. Dynamic tests and standardized static tests (3 or 4-point bending) allow the estimation of the modulus of elasticity (E) considering wood matter as homogeneous. Equations of motion do not take into account the presence of annual rings, the cellular pattern and local differences of density. A plant stem sample is a wave guide and the wave length associated to a longitudinal acoustic wave is about 1 m or more. At this scale the interaction wave – one stem is equivalent to an interaction wave – is equivalent to a homogeneous ‘stem,’ therefore reflections from tissues are negligible. The assessment of E_d for a plant stem sample is however difficult and can be a source of high measurement error: the stem is not perfectly straight and its diameter varies. The length and density of the sample can thus be biased. Nevertheless, acoustic testing allows a mean E to be obtained for a short, thick stem sample which cannot be tested through static testing where a long span distance between supports is required.

For our study, the signal analysis was based on time analysis with a sampling frequency set to 2.5MHz and an acquisition duration of 13.11ms (length of samples ranged from 40 cm to 80 cm). WISIS gives an estimation of the time of flight τ , which can be considered as the phase delay of the fastest wave travelling into the medium. E_d can be computed using the wave velocity (L/τ) and the mean density ρ of the material (Equation 1):

$$E_d = \rho \left(\frac{L}{\tau} \right)^2 \quad (1)$$

where L is the length of the sample. The second moment of area (I) was calculated for each sample tested and flexural stiffness (EI) obtained.

To determine if differences existed in species stem height, DBH and number of stems, analysis of variance was carried out along with post-hoc Fisher's Least Significant Difference (LSD) tests. For mechanically tested samples, E_d was examined as a function of stem length. To homogenise data, the position of the sample along the stem was calculated as a percentage of total stem length. These proportional data were then arcsine square root transformed prior to analysis. For I and E_d , the normality of distribution was tested using an Anderson-Darling test. If data were not normally distributed ($P < 0.05$), a logarithmic transformation was performed. Analysis of covariance was used to investigate the relationships in I , EI and E_d between species using stem length as a covariate.

Table 1 Mean height, DBH, number of stems per individual and bending strength for species present within six 100m x 4m transects traversing the avalanche path. Bending strength was not measured for all species. Letters in superscript indicate significant differences between species ($P < 0.05$). Species with fewer than nine individuals present were not included in the statistical analysis. Data are means \pm standard deviation.

Species	Number of individuals	Height (m)	Mean DBH of stems (mm)	Number of stems	Bending strength (MPa)	n (bending strength tests)
<i>Fagus sylvatica</i> L.	162	7.6 \pm 4.3 ^{acd}	82.0 \pm 54.2 ^a	3.2 \pm 4.0 ^a	55.1 \pm 18.1 ^{abc}	17
<i>Corylus avellana</i> L.	15	5.9 \pm 1.8 ^{abcd}	42.6 \pm 12.6 ^b	13.4 \pm 14.6 ^b	62.3 \pm 22.0 ^{abc}	17
<i>Alnus incana</i> (L.) Moench	9	5.4 \pm 2.0 ^{abcd}	52.0 \pm 11.6 ^{ab}	3.9 \pm 2.6 ^{ac}	35.1 \pm 9.1 ^{bd}	14
<i>Alnus viridis</i> (Chaix) DC.	4	2.9 \pm 0.9	33.2 \pm 9.8	12.5 \pm 11.2	27.8 \pm 5.9 ^d	11
<i>Betula pendula</i> L.	27	6.9 \pm 2.4 ^{abc}	80.7 \pm 49.4 ^{ab}	1.5 \pm 1.4 ^{ac}	47.2 \pm 15.9 ^{bcd}	8
<i>Salix appendiculata</i> Vill.	23	5.6 \pm 2.4 ^{bcd}	75.4 \pm 31.9 ^{ab}	2.5 \pm 3.5 ^{ac}	-	-
<i>Quercus petraea</i> Liebl.	20	5.9 \pm 3.6 ^{abcd}	78.6 \pm 46.5 ^{ab}	1.0 \pm 0.2 ^c	-	-
<i>Pinus sylvestris</i> L.	6	2.9 \pm 2.4	63.5 \pm 46.7	1.0 \pm 0.0	-	-
<i>Picea abies</i> (L.) H. Karst.	36	4.8 \pm 3.3 ^{bd}	73.6 \pm 48.2 ^a	1.1 \pm 0.4 ^c	-	-
<i>Populus tremula</i> L.	2	3.1 \pm 0.5	39.0 \pm 11.3	1.0 \pm 0.0	-	-
<i>Acer pseudoplatanus</i> L.	2	7.3 \pm 1.9	72.0 \pm 25.5	2.0 \pm 0.0	-	-
<i>Prunus avium</i> (L.) L.	6	9.9 \pm 2.1	111.7 \pm 60.9	1.3 \pm 0.8	-	-
<i>Fraxinus excelsior</i> L.	3	7.0 \pm 1.1	81.3 \pm 23.8	1.0 \pm 0.0	-	-

Results

F. sylvatica was the most abundant species growing at the edge and near the avalanche path (Table 1). Several species, including *A. viridis* were present in very low numbers. *A. viridis* was only observed at the centre and edges of the path. *A. incana* was located on the avalanche debris downslope, along with *B. pendula* which was occasionally observed further upslope but not within the immediate vicinity of the avalanche path. *C. avellana* was present at the edges of the avalanche path and possessed the greatest number of stems compared to all other species. Apart from *P. abies* and *B. pendula*, single-stemmed trees (*Q. petraea*, *P. sylvestris*, *P. avium*, *F. excelsior*, *P. tremula*), were present in low numbers within transects (Table 1).

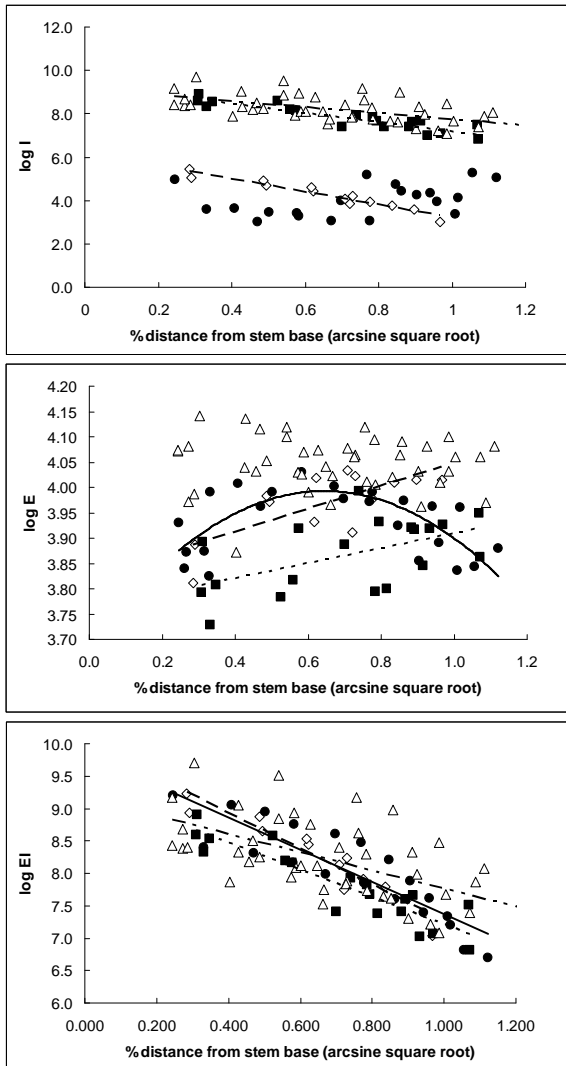


Fig. 2a) Logarithmic second moment of area ($\log I$) decreased significantly with relative distance from the stem base in all species examined except for European beech. $\log I$ was significantly greater in hazelnut (white triangles and dashed and dotted line) and Green alder (black squares and dotted line) compared to European beech (black circles) and silver birch (white diamonds and dashed line) ($P < 0.05$).

b) Logarithmic dynamic modulus of elasticity ($\log E$) was lowest at the stem base for all species except hazelnut, where it remained constant along the stem. In Silver birch and Green alder, E_d increased significantly from the stem base towards the apex. In European beech (solid line), E_d increased significantly along the stem length up to approximately 50% of the length before then decreasing.

c) Logarithmic flexural stiffness ($\log EI$) decreased significantly with distance from the stem base in all species ($P < 0.05$).

$\log I$ decreased significantly with relative distance from the stem base in all species examined except for *F. sylvatica* (Figure 2a, Table 2). $\log I$ was significantly greater in *C. avellana* and *A. viridis* compared to *F. sylvatica* (Figure 2a, Table 2). Bending strength was highest in *C. avellana* and *F. sylvatica* and lowest in *A. viridis*, with *A. incana* and *B. pendula* having intermediate values (Table 1). E_d was highest in *C. avellana* and lowest in *A. viridis* (Figure 2b, Table 2). In *B. pendula* and *A. viridis*, E_d increased linearly from the stem base to the apex and in *F. sylvatica*, E_d increased significantly along the stem length up to approximately 50% of the length before then decreasing (Figure 2b, Table 2). In *C. avellana*, E_d remained constant along the stem (Figure 2b, Table 2). In all species, $\log EI$ decreased significantly from the stem base to the apex (Figure 2c, Table 2).

Table 2 Regression equations, R^2 and probability (P) for the regressions shown in Figure 2a,b, and c.

Species	$\log I$			$\log E$			$\log EI$		
	Regression	R^2	P	Regression	R^2	P	Regression	R^2	P
<i>F. sylvatica</i>	$-1.89x+5.40$	66	<0.001	$-0.71x^2+0.92x+3.69$	47	0.001	$-1.91x+9.34$	64	<0.001
<i>C. avellana</i>	$-1.39x+5.11$	39	<0.001	$-0.02x+4.05$	1	0.551	$-1.41x+9.17$	37	<0.001
<i>A. viridis</i>	$-2.11x+9.32$	83	<0.001	$0.15x+3.76$	29	0.017	$-2.11x+9.32$	83	<0.001
<i>B. pendula</i>	$-2.99x+5.21$	86	<0.001	$0.23x+3.82$	54	0.004	$-2.77x+10.0$	90	<0.001

Discussion

The most common species found within and around the avalanche path possessed the ability to produce numerous stems, with the shrubs *C. avellana* and *A. viridis* having a highly multi-stemmed form. *F. sylvatica* demonstrated a strong morphological plasticity as both arborescent and shrubby forms co-existed, the latter being found at the edges of the avalanche path. *B. pendula* was rarely found near the centre of the path and was more abundant downslope of the path. Species with single stems generally grew at a distance or downslope of the avalanche path. Therefore, the ability to multi-stem in response to snow disturbance is likely an important survival strategy for trees growing in subalpine zones. Larger, single-stemmed trees will be more likely to fail if they cannot bend during an avalanche [6], resulting in death of the individual. By possessing the ability to regenerate new stems from the existing main stem or stem-root base, individuals will persist in the landscape, and not rely on seeding to remain dominant.

A. viridis had the lowest mean σ and E_d , and particularly low values of E_d at the stem base, thus enabling this species, generally found at the centre of avalanche paths, to bend easily during an avalanche disturbance, reducing the likelihood of stem breakage or uprooting. *C. avellana* and *F. sylvatica*, found at the edges of avalanche paths, possessed the highest mean E_d and σ . These two species may better resist the weight of the snow, compared to *A. viridis*, but were less flexible at the stem base. In all species except *C. avellana*, where E_d remained constant in stems, E_d increased from the stem base to the apex and in all individuals, EI decreased from the base to the apex, with little difference between species.

Usually, E decreases from old to younger stems in self-supporting plants such as trees and shrubs, therefore the stem bases of trees are mostly stiffer than the apical branches [10,11]. However, the stem bases might contain a transition zone between the stem and roots, and roots have lower E than stem wood [12]. In two populations of *A. viridis* from the Alps in Switzerland and the Black Forest Forest, Germany, Brüchert et al [13] found that E decreased with decreasing stem age, therefore E was higher at the stem base. It was not stated whether these populations were perturbed by frequent disturbance. In our study, stem bases of trees may be damaged by avalanches and debris entrained by the avalanche, resulting in scars and decayed wood which reduces E . Tension wood was probably present in large amounts along stems, but E in tension wood is usually higher than that of normal wood [14]. A further explanation for the increase in E up the stem in *B. pendula*, *A. viridis* and to a certain extent, *F. sylvatica*, is that when the snow melts in the spring, apical stem parts need to grow towards the dominant source (outwards and upwards, depending on slope angle and orientation). Being materially stiffer would allow these young stems to quickly form a canopy and benefit from most available light during the short subalpine growing season. Stem bases of the same species are larger and usually procumbent and therefore would need more time and energy to straighten up. If avalanches are frequent, plastic deformation of the stem base will occur and plant response to the frequent disturbance may be to invest little in wood structure or straightening up mechanisms from the stem base. In *A. viridis*, vegetative reproduction is common, and roots can grow from the prostrate stems [15]. An increase in E along the stem can also be found in climbing species such as lianas, where the ‘searcher

shoots' are relatively stiff compared to the basal parts of the stem, allowing individuals to find suitable supports for growth towards the canopy [10].

The differences in E along the stem observed between species may indicate differences in strategies for forming tension wood, which are known to occur at least between *F. sylvatica* and *A. incana* in experiments simulating substrate mass movement [16]. Tension wood efficiency also differs between species [17]. Although E increased along the stem in three species, it remained constant along the stem in *C. avellana*. *C. avellana* possessed significantly more stems than any other species at the site, and the stems were often leaning on each other, thus providing mutual support. A similar situation can be found in semi-self-supporting plants (species which often lean on the surrounding vegetation, rather than climbing via twining or tendrils), where E often remains unchanging and values can be relatively high in both young and old growth stages [10,11].

E augments significantly with a decrease in temperature [6, 18], therefore future experiments should focus on how E changes with temperature, and if this mechanical behaviour differs between species. We will also examine how mechanical properties and stem allometry change along the altitudinal gradient of the avalanche path and test the behaviour of conifer species present near path. The age of individuals will be determined using dendrochronological techniques and xylem structure along the stem examined.

Acknowledgements

Funding was received from INRA (Jeune Equipe), France. Thanks are due to D. Guibal and G. Chaix CIRAD, France, C. Atger (Pousse Conseil), M. Ghestem (Ministère d'Agriculture) and Z. Mao, Montpellier 2 University, France, for experimental help and to F. Munoz Montpellier 2 University, France, for species identification. AMAP (Botany and Computational Plant Architecture) is a joint research unit which associates CIRAD (UMR51), CNRS (UMR5120), INRA (UMR931), IRD (2M123), and Montpellier 2 University (UM27).

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